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Transient Masculinization in the Fossa, *Cryptoprocta ferox* (Carnivora, Viverridae)[1]

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ABSTRACT

In at least 9 mammalian species, females are masculinized throughout life, but the benefits of this remain unclear despite decades of thorough study, in particular of the spotted hyaena (*Crocuta crocuta*) in which the phenomenon has been associated with a high fitness cost. Through examination of wild and captive fossas (*Cryptoprocta ferox*, Viverridae), androgen assays, and DNA typing for confirmation of gender, we made the first discovery of transient masculinization of a female mammal. Juvenile female fossas exhibited an enlarged, spinescent clitoris supported by an os clitoridis and a pigmented secretion on the underpart fur that in adults was confined to males. These features appeared to diminish with age. The majority of adult females lacked them, and os clitoridis length was inversely related to head-body length. No evidence was found to link this masculinization to elevated female androgen levels. Circulating concentrations of testosterone and androstenedione, but not dihydrotestosterone, were significantly lower in females than in males. No significant differences in testosterone, androstenedione, or dihydrotestosterone levels were found between juvenile (masculinized) and adult (nonmasculinized) females. There are several possible physiological mechanisms for this masculinization. None of the hypotheses so far proposed to explain the evolutionary basis of female masculinization in mammals are applicable to our findings. We present 2 new hypotheses for testing and development.

behavior, female reproductive tract, male reproductive tract, penis, puberty, steroid hormones, testosterone

INTRODUCTION

Females of several mammal species are masculinized throughout life, including moles (*Talpa*) [1, 2], spotted hyaenas (*Crocuta crocuta*) [3], and a number of less thoroughly investigated primate genera (e.g., *Ateles*, *Allouatta*, *Cebus*, and *Lagothrix*) [4, 5]. In the most well-studied species, the spotted hyaena, such masculinization leads to difficulties the first time a female gives birth, estimated as a lifetime fitness cost of 16–25% [6]. A substantial, obvious benefit that would outweigh such a cost is to be expected, yet for no mammal species has the adaptive value of female masculinization been clearly established.

Two groups of explanations for female masculinization in mammals have been proposed (reviewed in [7, 8]). The first group applies to species where increased aggression confers higher female fitness. Female masculinization has been interpreted as a nonadaptive consequence of raised androgen levels, which are thought to be selected for because they raise aggression levels. Studies of androgen levels in 2 species exhibiting female masculinization support this view. In the spotted hyaena, female levels of circulating androstenedione are at least equal to [8, 9] if not higher than [10, 11] male levels (reviewed in [8]). In the European mole, *Talpa europaea*, levels of circulating testosterone in females approach those in males outside the breeding season, being exceptionally high relative to those in other nonpregnant female mammals [12]. Aggression is thought to benefit the spotted hyaena female either as a neonate in promoting siblicide [13] or as an adult in mediating high social rank [7]. It has been suggested that the female mole (*Talpa europaea*) benefits from aggression during territorial disputes [14]. The alternative group of explanations for mammalian female masculinization includes proposals that masculinization itself could directly benefit female fitness. Wickler [15] and Kruuk [16] considered the masculinized genitalia of the female spotted hyaena as essential to the greeting ceremony that maintains individuals in a social group. East et al. [13] proposed that the form of the genitalia gives an adult female hyaena control over mating, leading to beneficial male submission within the group.

Masculinization in 2 female museum specimens of the fossa (*Cryptoprocta ferox*) was described early in the last century [17, 18]. The fossa is a large, solitary civet endemic to Madagascar, with a head-body length of approximately 70 cm [19]. To confirm these reports, we examined genital morphology in individuals of both sexes and a range of ages from a wild population and a captive group. To investigate the physiological basis and to identify possible adaptive benefits of any observed masculinization, we also measured androgen levels of individuals in the wild population.

MATERIALS AND METHODS

Capture, Examination, and Age Determination

Forty-three fossas were captured with box traps in Kirindy Forest, a dry deciduous forest in western Madagascar (20°4′S, 44°39′E) during 1994–1996. Trapping was concentrated in the dry season (May–October) after wet season trapping was found to generate a very low capture rate. Trapped animals were anesthetized with 5 mg ketamine and 1 mg xylazine per kilogram of body weight. Head-body length was measured. The os penis in males and the os clitoridis in females were located by palpation (the os clitoridis could also usually be clearly seen through the skin) and measured using callipers. Length of a testis was measured with callipers at the longest point. The quantity of orange secretion apparent on the underpart fur was scored by eye in terms of extent and depth of color (0–

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5): 0 = no orange perceptible anywhere on the underpart fur; 1 = orange just perceptible in at least 1 area of the underpart fur; 3 = clearly orange in certain areas of the underpart fur; 5 = all underpart fur an intense orange. Individuals with orange secretion midway between 1 and 3 were scored as 2, and those midway between 3 and 5 were scored as 4. Age was assessed by scoring tooth wear (0–5): 0 = no toothwear perceptible; 1 = 1 small indication of toothwear, e.g., 1 tip missing; 3 = clear signs of light wear, e.g., many tips missing; 5 = heavy wear on all teeth, discoloration. Scores of 2 and 4 for tooth wear were intermediate to 1 and 3, and 3 and 5, respectively. Adult females were examined for mammary development as an indicator of late pregnancy or lactation. This examination was done simply to confirm captive data and limited observations in the wild indicating that the reproductive season is exclusive to the wet season; pregnancy was not expected because most trapping was carried out during the dry season. Juveniles were distinguished by their small head-body length, unsuckled mammae, low level of tooth wear, and in those less than 20 mo of age, the presence of milk teeth. Because the fossa is a seasonal breeder, it was possible to age juveniles precisely (to the month) through presence/absence of milk teeth and head-body length [20]. In captive animals, maturity is reached at 3–4 yr of age [20, 21].

Because all wild-caught juvenile females were over 10 mo old, 3 captive-born female fossas held at Suffolk Wildlife Park, U.K., were monitored bimonthly from the age of 10 wk in September 1997 until the age of 10 mo. The 3 females were from the same natal group and were kept together with their single brother throughout the monitoring period. Anesthesia was not permitted, precluding accurate measurements, but the underpart secretion was scored, the clitoris was examined, and when feasible, attempts were made to estimate os clitoridis length with a combination of palpation and callipers. The underpart secretion and genitalia of the young male were similarly monitored.

Confirmation of Sex by DNA Typing

Ear disks were collected during ear tagging of wild-caught fossas. Total cellular DNA was extracted [22] from ear disks and used to detemine the sex of each animal by polymerase chain reaction (PCR) detection of the male-specific *SRY* gene as described previously [23]. PCR detection of 5 microsatellites [24] provided a positive control for PCR function in females.

Androgen Assays

Between June 1995 and September 1996, blood samples were collected from fossas at the place of capture into heparinized vacutainers and centrifuged for 10 min. The volumes of the resulting plasma samples were recorded prior to storage in cold water until arrival at base camp (<16 h), where steroids were extracted into methanol by passage through Sep-Pak Plus C18 cartridges (Millipore U.K. Ltd., Watford, U.K.) and refrigerated. This step was carried out to protect the steroids from damage by hostile conditions and bacterial breakdown in the field.

In Aberdeen, in June 1997, all samples were dried in air at 37°C prior to reconstitution in 2 ml of DELFIA assay buffer (PerkinElmer Life Sciences, Cambridge, U.K.), a Tris-HCl buffered NaCl solution, pH 7.8, containing <10% BSA, bovine γ globulins, Tween 40, diethylenetriaminepentaacetic acid, and an inert red dye. The recovery of testosterone from adult male human blood following the Sep-Pak extraction was 92%. Androstenedione was measured using a single Coat-a-Count extraction androstenedione kit (EURO/DPC Ltd., Caernarfon, U.K.). Because the blood samples had already been extracted into methanol, the ethyl ether extraction step was omitted. Testosterone was measured using a single DELFIA kit (PerkinElmer Life Sciences), substituting DELFIA assay buffer for kit buffer and the testosterone reference preparation T1268 (Sigma-Aldrich Co. Ltd., Poole, U.K.), made up in methanol, dried, and reconstituted in DELFIA assay buffer. Dihydrotestosterone was measured using a single dihydrotestosterone kit (DSL U.K. Ltd, Tooting, U.K.), with 400-μl aliquots of each reconstituted fossa sample used for oxidation and hexane/ethanol extraction steps carried out according to kit instructions.

The recovery of added steroids from fossa plasma was linear and proportional, and the serial dilution of fossa plasma was parallel to each standard curve (Fig. 1). The recovery of standard added with sample was 97.0% for testosterone, 96.9% for androstenedione, and 97.4% for dihydrotestosterone. For each hormone, all samples were determined in a single assay. The preliminary assay of randomly selected samples enabled the dilution of the samples where appropriate so that all androgen values determined for the fossa samples fell within the ranges of the standard curves. Because the androgen concentrations were measured in single assays, typical assay performance figures are given. Specifically, the sensitivities and intra-assay coefficients of variation were 0.4 nmol/L and 4–8% for testosterone, 0.07 nmol/L and 5–8% for androstenedione, and 14 pmol/L and 3–6% for dihydrotestosterone, repectively. Cross-reactivities for the assay kits are 0.2% and 12.0% for testosterone with androstenedione and dihydrotestosterone, respectively; 1.9% and 0.02% for dihydrotestosterone with androstenedione and testosterone, respectively; 0.2% and 0.2% for androstenedione with testosterone and dihydrotestosterone, respectively. From 22 individuals, more than 1 sample was obtained on different occasions. For each of these, the median value was used in the analyses.

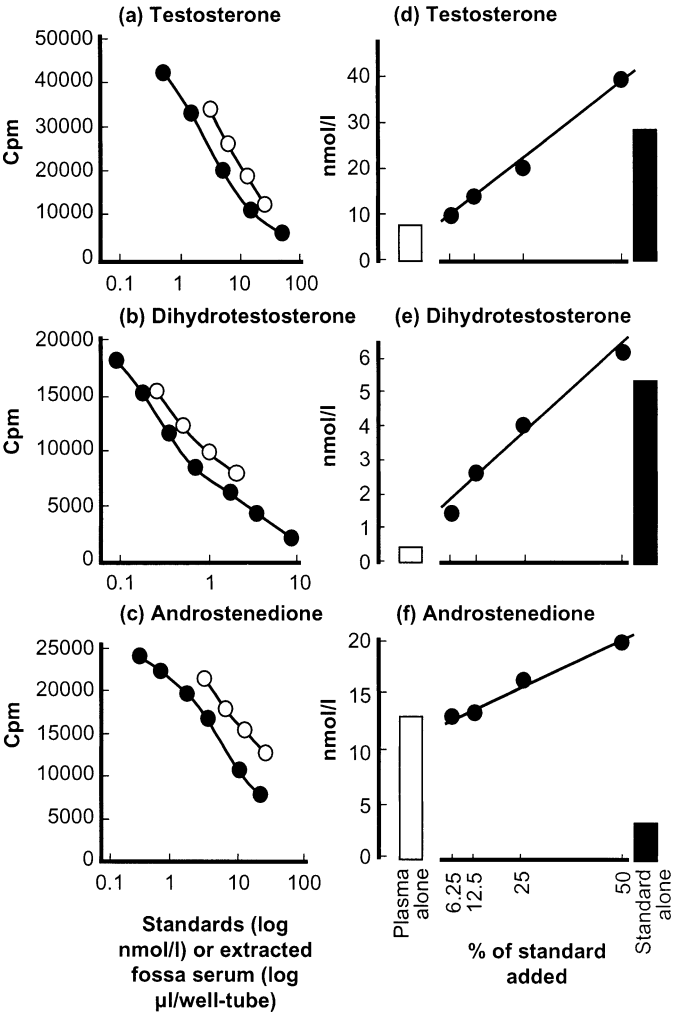

FIG. 1. Dose responses for extracted fossa plasma assayed for testosterone (μl extracted plasma/well) (**a**), dihydrotestosterone (μl extracted plasma 10^{-1} $tube^{-1}$) (**b**), and androstenedione (μl extracted plasma/tube) (**c**), demonstrating parallelism with the assay kit standard curves. Dose responses for serially diluted assay standard preparations from the testosterone (**d**), dihydrotestosterone (**e**), and androstenedione (**f**) assay kits doped with fixed quantities of extracted fossa plasma demonstrate linear and proportional recovery of each steroid.

Data Analysis

Secretion scores were expressed as medians with ≥95% nonparametric confidence intervals (CIs) obtained using the binomial distribution [25]. The same method was used to compare androgen levels graphically, but using ≥80% CIs because of the smaller sample sizes. Scores and androgen levels were compared between males and females and between adults and juveniles using the Mann-Whitney *U*-test. Os clitoridis lengths of adult and juvenile females were compared using an unpaired two-tailed *t*-test. Various correlations between androgen levels, morphological measurements, and scores were tested using the Spearman rank correlation procedure.

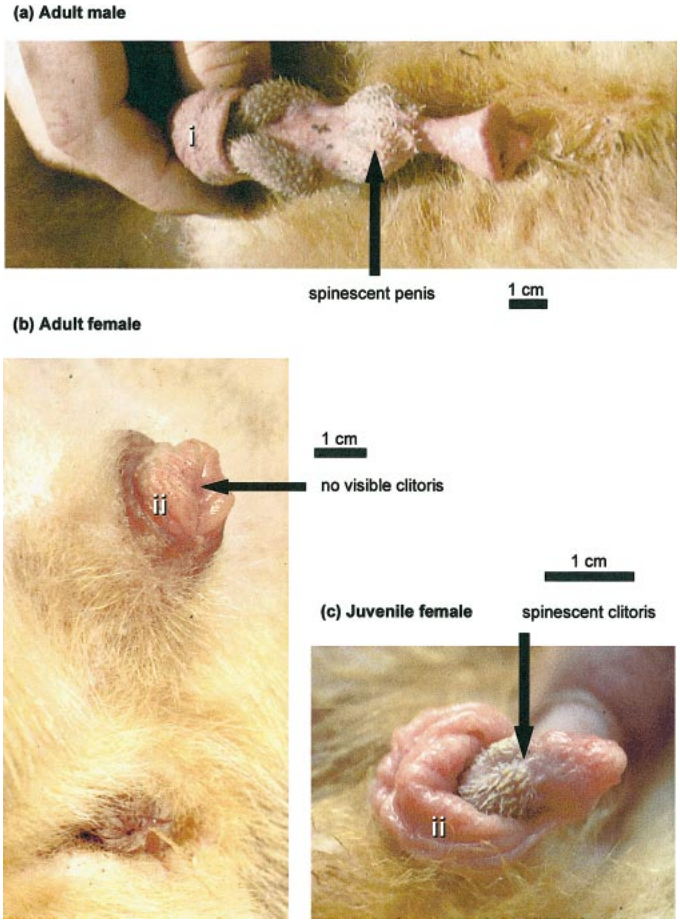

FIG. 2. External genitalia of the fossa: male (**a**), adult female (**b**), and juvenile female (**c**). In the male, the sheath (i) is pulled back to the base of the penis to reveal the spines on the posterior two thirds of the erect shaft. In the 2 females, the labia (ii) are similarly pulled back, revealing the lack of visible clitoris in the adult and the substantial, spinescent clitoris in the juvenile.

RESULTS

We examined 43 wild-caught fossas: 18 adult males, 7 juvenile males, 10 adult females, and 8 juvenile females. As expected, none of the adult females was perceptibly pregnant or lactating; only 1 of them was caught during the reproductive season. Juvenile males ranged in age from 8 mo to 31 mo, and juvenile females ranged from 12 mo to 33 mo; 1 female 40 mo of age was also classed as a juvenile because of her nonparous state and a tooth wear score of 0. We also examined a litter of 4 captive-born juveniles: 1 male and 3 females.

Wild-caught individuals were sexed without difficulty in the field, and the sex of these individuals was confirmed by DNA typing for the male-specific *SRY* gene. Each adult male fossa (Fig. 2a) had prominent testes and a large penis. The latter was supported by a bone, and the drawing back of the sheath revealed a profuse covering of hard spines along the basal two thirds of its length. A mildly pungent orange (Mars Orange [26]) secretion stained the cream-colored fur between the throat and anus of the adult males, especially between the forelimbs and the hind limbs. All 7 wild-caught and the single captive-born juvenile male fossas resembled the adult males in all these features, including secretion score (Table 1), except that their genitalia were not as large relative to body size; the ratio of testis length:head-body length differed significantly between adults and juveniles (Mann-Whitney $U' = 108$, $P < 0.001$), as did the ratio of os penis length:head-body length ($U' = 53$, $P < 0.001$). The 10 wild-caught adult females (Fig. 2b) lacked all but 1 of these features: 4 of these females possessed a small bone (os clitoridis) within the tip of the clitoris, which was hard and inflexible when palpated. All adult females had cream-colored (Ivory Yellow [26]) underparts, with little or no perceptible orange secretion.

In contrast with the adult females, all 8 wild-caught juvenile females (Fig. 2c), although easily distinguishable from males, possessed several masculine features. The clitoris was substantially enlarged relative to that of the adult female and was supported in all individuals by an os clitoridis that was significantly larger than that found in the 4 adult females (Table 1; $t_8 = 5.703$, $P < 0.001$). The anterior of the clitoris base was covered with spines (or in 1 animal a hard crust) in 6 individuals. A raised, naked region, reminiscent of a penis raphe, lay between the anus and the genital opening, and the secretion score was significantly higher than that in adult females (Table 1; Mann-Whitney $U' = 7$ 1.5, $P < 0.01$).

Very young female fossas showed little masculinization. At the first examination, at the age of 10 wk, the only masculine feature apparent in the captive-born females was an os clitoridis. This bone was present in only 2 of the 3 individuals and, at an estimated 2–4 mm long, was clearly smaller than that found in the older wild-caught juveniles. By the age of 7 mo, each female had an enlarged clitoris, an os clitoridis of estimated length 10–15 mm, and tiny (~1 mm long) spines at the clitoris base but still exhibited little or no underpart secretion by the age of 10 mo, when examination ended.

These masculine features appeared to be transient in females and were most pronounced in the second and third years of life. None of the features, apart from the os clitoridis in a reduced form, was found in any adult female,

TABLE 1. Key masculine features in fossas according to sex and age class.

	Adult		Juvenile	
Feature	Male	Female	Male	Female
Os penis/clitoridis length (mm)*†	72.2 ± 9.6 (n = 17)	0 (n = 6) 5.5 ± 3.3[a] (n = 4)	47.4 ± 9.7	14.5 ± 5.0[b]
Spinescent penis/clitoris	Yes	No	Yes	Yes (n = 5) No (n = 3)
Secretion†‡	4 (3.5–4.5)	0.75 (0–1)[a]	4 (2–5)	3.25 (0–5)[b]
Sample size§	18	10	7	8

* Mean ± SD.
† Different superscripts indicate significant differences.
‡ Median score (0–5 scale) with 95% CI.
§ Sample sizes as stated unless otherwise specified.

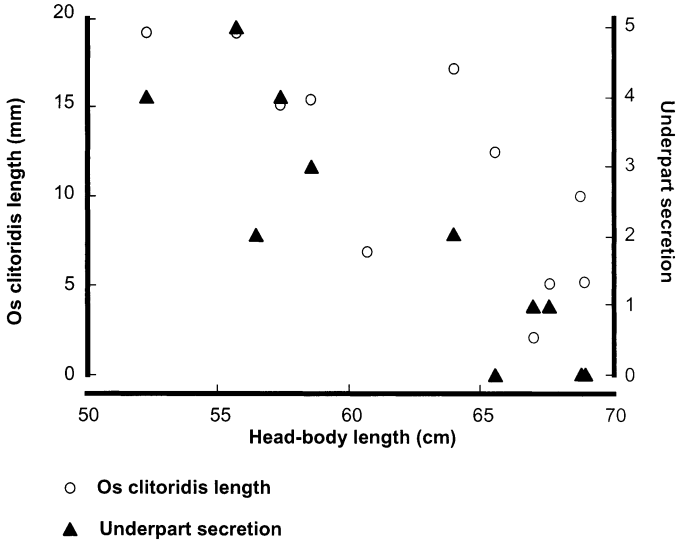

FIG. 3. Os clitoridis length (mm) and quantity of secretion apparent on the underparts (scored as 0–5 by eye) versus head-body length (cm) in all female fossas possessing an os clitoridis: 4 adults and 7 juveniles (os clitoridis data were omitted for 1 juvenile in which the os clitoridis was not measured).

and the features were also reduced in females <1 yr old. Head-body length of females with an os clitoridis was negatively correlated with both os clitoridis length (Spearman rank correlation: $r_s = -0.839$, $P < 0.02$, n = 10) and secretion score ($r_s = -0.882$, $P < 0.01$, n = 11) (Fig. 3). Three of the 4 adult females possessing an os clitoridis had the lowest tooth wear scores for adults, indicating that they were relatively young.

We found no evidence that masculinization of female fossas is androgen dependent. Blood samples taken from 13 adult male, 10 adult female, 4 juvenile male, and 6 juvenile female wild-caught fossas were assayed for 3 androgens: androstenedione, testosterone, and dihydrotestosterone (Fig. 4). In both juveniles and adults, median androstenedione and testosterone levels were higher in males than in females (Mann-Whitney *U*-test, androstenedione: juveniles $U' = 24$, $P < 0.05$, adults $U' = 130$, $P < 0.0001$; testosterone: juveniles $U' = 22$, $P < 0.05$, adults $U' = 103$, $P < 0.02$), although the difference was not significant for dihydrotestosterone levels in either age class. No significant differences were found between juvenile and adult levels of any androgen in either females or males (Mann-Whitney *U*-test, $P > 0.05$). No significant relationship was found between levels of any androgen and os clitoridis length (Spearman rank correlation, $P > 0.05$, n = 9) or secretion score within females (Spearman rank correlation, $P > 0.05$, n = 16).

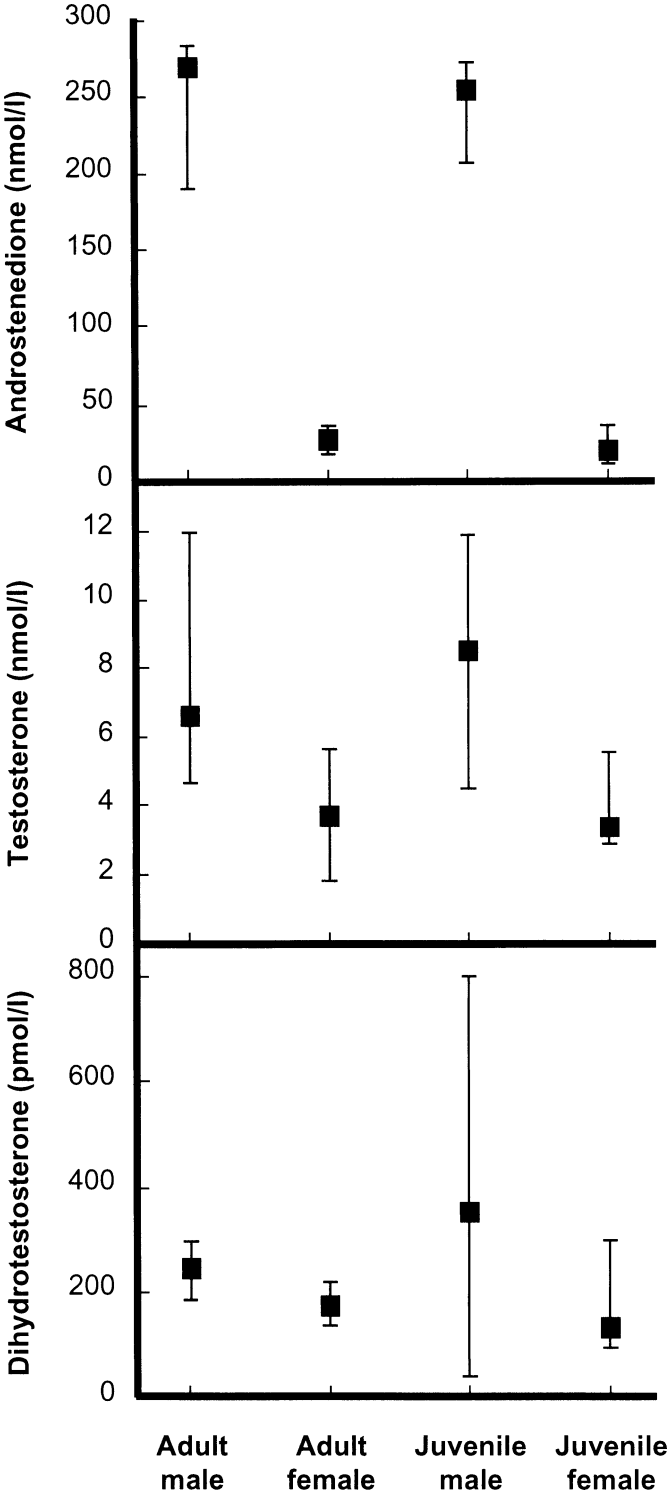

FIG. 4. Median levels of plasma concentrations of androstenedione (nmol/L), testosterone (nmol/L), and dihydrotestosterone (pmol/L) in 13 adult male, 10 adult female, 4 juvenile male, and 6 juvenile female fossas, with confidence limits of ≥80%.

DISCUSSION

Uniquely among all mammals so far examined, masculinization in the female fossa appears to be a transient feature, most pronounced in juveniles 1–2 yr of age. In captivity, the mother is aggressive towards her young once they reach the age of 12 mo (A. Winkler, personal communication). This observation and the fact that all but 1 wild-caught juvenile were at least 12 mo old suggest that 12 mo is the age at which juveniles become independent of the mother and disperse, the females retaining their masculine features until they reach sexual maturity at 3–4 yr.

The form of masculinization we observed corresponds in all aspects to the descriptions by Lönnberg [17] and Carlsson [18] of their respective single specimens with 3 exceptions. Lönnberg described a pseudoscrotum, but neither author described the underpart secretion. Carlsson's specimen appeared to be an adult, and Carlsson noted small glandular elevations behind the vulva but did not judge these to constitute a pseudoscrotum. Vosseler [27] noted the

underpart secretion and that males possessed it in greater quantity than did females. No previous author, however, has identified the masculinization as transient. Klockenkämper [28] identified another feature exclusive to males and juvenile females: anogenital scent marking outside (rather than only during) the mating season.

No previous hypothesis proposed to explain masculinization of female mammals appears directly applicable to the fossa. In species where increased aggression in females confers higher fitness, it has been proposed that female masculinization is a nonadaptive consequence of selection for increased androgen levels. There is, as yet, no reported evidence in the sparse literature that increased aggression confers higher fitness in female fossas. Adult females appear to have home ranges that are more exclusive than those of adult males [19], suggesting that females may be more territorial, but this territoriality does not appear to be extreme. We found no other information on fossa aggression levels, other than from workers at Duisburg Zoo (A. Winkler, personal communication) who observed that the mother becomes aggressive towards her young when they reach 1 yr of age, that the adult female is sometimes aggressive to the adult male, and that very rarely a juvenile may become aggressive to a same-sex sibling over food.

We found no evidence that androgen levels are elevated in masculinized juvenile female fossas compared with nonmasculinized adult females (Fig. 4). In addition, levels of circulating testosterone and androstenedione were significantly lower in juvenile female fossas than in juvenile males, and the same was true in adults. Fossas thus differed from both spotted hyaenas and European moles. In spotted hyaenas, female androstenedione levels are consistently at least equal to those of males throughout the year. In European moles, testosterone levels of females approach those of males outside the reproductive season. Fossas also differ from spotted hyaenas in that, unlike young spotted hyaenas, young female fossas exhibited very little masculinization; thus, it is doubtful that the phenomenon is brought about in the fetus by elevated maternal androgens. Overall, the median androgen concentrations of adult female fossas (testosterone: 1.1 ng/ml, ≥95% CI = 0.4–1.7 ng/ml; androstenedione: 8.2 ng/ml, ≥95% CI = 4.5–15.4 ng/ml) appeared to be high relative to those in other female mammals [8, 11, 12]). However, comparisons of circulating androgen levels with those presented in other studies are of limited value because there has been no cross-comparison of the diverse assay systems used.

In some mammal species, masculinization or virilization is independent of the conversion of circulating testosterone to dihydrotestosterone, such as in the male pouch young of the tammar wallaby (*Macropus eugenii* [29]). For this species, it has been hypothesized that conversion of prohormones to androgens is increased within the target tissues; this hypothesis could be applied also to the fossa. Juvenile female fossas could have increased androgen receptor activity in the genital area, ventral skin, and perhaps the brain or increased 5α-reductase activity in target tissues. In the latter case, the tissue-specific conversion of testosterone to dihydrotestosterone would be increased. It is also possible that androgens are not involved in female fossa masculinization. For instance, masculinization of female neonate hyaena genitalia occurs to some extent even when treated throughout development with androgen inhibitors [30]. Through another apparently androgen-independent process, tissue that forms the pouch of the tammar wallaby will, in the absence of two X chromosomes, develop into a scrotum [31].

If androgen levels are not raised, the alternative explanation is that there are direct benefits of the masculinization. However, the benefits so far proposed (participation in the greeting ceremony, female dominance) apply to females in the context of a socially structured group, whereas the fossa is solitary [19]. Furthermore, the benefit that East et al. [13] proposed for female hyaenas, that the resulting impossibility of rape leads to beneficially submissive behavior by males, could not be expected in the fossa. Masculinized fossa females are not yet fertile; thus, males would gain no fitness advantage from being allowed to mate with them and therefore would not benefit from such behavior.

We propose instead 2 hypotheses for future testing that are more suited to the transient nature of the masculinization and to the solitary nature of the fossa. First, transient masculinization could enable juvenile female fossas to avoid sexual harassment by adult males, as in masculinized insect females [32, 33]. Sexual harassment is a common phenomenon in mammals, and its costs may include injuries or fatalities [34]. Female fossas are sparsely distributed and have only a brief annual estrus. Both factors may encourage males to force copulation on any female they encounter. Juvenile females are especially vulnerable because of their small size and recent independence from the mother. A masculine appearance could allow them to escape detection or could signal to males that they are not a potential mate. In addition, the genitalia would obstruct copulation. Second, transient masculinization could enable juvenile female fossas to escape another form of aggression, that from territorial females. Radiotracking data indicate that females have exclusive ranges [19], whereas males are less territorial. A dispersing female may be viewed as a threat by a territorial female. All females of dispersing age in our study were masculinized, which may allow them to escape detection and attack by territorial females.

Both hypotheses are based on the idea of the juvenile female benefitting from her gender being less conspicuous to a potential attacker. Neither hypothesis, however, explains what the juvenile female gains from anogenital scent marking outside the mating season, like males [28]. Little research had been carried out on the fossa in the wild until Hawkins [19] conducted a 2-yr study. The findings from that study and those of studies on captive individuals [20, 21] have provided sufficient data to reject previous hypotheses, but further research is required to test and develop more appropriate hypotheses.

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